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Original Article

Integrating network analysis, sensor tags, and observation to understand shark ecology and behavior

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Group living in animals is a well-studied phenomenon, having been documented extensively in a wide range of terrestrial, freshwater, and marine species. Although social dynamics are complex across space and time, recent technological and analytical advances enable deeper understanding of their nature and ecological implications. While for some taxa, a great deal of information is known regarding the mechanistic underpinnings of these social processes, knowledge of these mechanisms in elasmobranchs is lacking. Here, we used an integrative and novel combination of direct observation, accelerometer biologgers, and recent advances in network analysis to better understand the mechanistic bases of individual-level differences in sociality (leadership, network attributes) and diel patterns of locomotor activity in a widespread marine predator, the lemon shark (*Negaprion brevirostris*). We found that dynamic models of interaction based on Markov chains can accurately predict juvenile lemon shark social behavior and that lemon sharks did not occupy consistent positions within their network. Lemon sharks did however preferentially associate with specific group members, by sex as well as by similarity or nonsimilarity for a number of behavioral (nonsimilarity: leadership) and locomotor traits (similarity: proportion of time swimming "fast," mean swim duration; nonsimilarity: proportion of swimming bursts/transitions between activity states). Our study provides some of the first information on the mechanistic bases of group living and personality in sharks and further, a potential experimental approach for studying fine-scale differences in behavior and locomotor patterns in difficult-to-study organisms.

Key words: **accelerometry, intermittent locomotion, Markov chains, network position, personality.**

INTRODUCTION

Understanding why animals move and how the spatial and temporal structures of these activities relate to their ecology and evolution has been a long-standing research challenge in behavioral biology (Patterson et al. 2008). Of particular value to researchers are experimental or conceptual approaches that attempt to ascertain the links between individual-level differences in movement and other aspects of an animal's behavioral repertoire (i.e., personality, Cote et al. 2010; Wilson and Godin 2010) including, in gregarious species, their social dynamics (Wilson, Krause, et al. 2014). However, these approaches, particularly when attempted in nature, are commonly beset by a number of logistical problems. Free-ranging animals are often secretive, cryptic, and/or highly mobile making data collection difficult if not impossible in many instances (Altmann 1974; Costa and Sinervo 2004). As a possible solution to the conundrum of observing animals when they cannot be "seen," electronic tagging technologies (both biotelemetry and biologging

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platforms) are frequently used to quantify habitat use and activity patterns in a diverse range of species and environments (Cooke et al. 2004; Brown et al. 2013). Similarly, innovations in biological sensor tags that quantify aspects of animal "state" (i.e., heart rate, body temperature, tissue biochemistry and appendage activity) offer new opportunities to quantify individual-based dynamics (Cooke et al. 2004; Payne et al. 2014). Although these data offer exceptional value with respect to spatial ecology, they are often difficult to interpret in terms of ecological data that involves interindividual interactions (mating, agonistic, cooperative and competitive exchanges) (Jacoby, Brooks, et al. 2012).

Social network analysis, in conjunction with electronic tags, offers a valuable and novel opportunity to study patterns of social affiliation in both "seen" and "unseen" free-ranging animals within the context of their natural environment (Krause et al. 2011; Jacoby, Croft, et al. 2012; Brown et al. 2013). Network analysis acknowledges the complex nature of relationships between multiple interacting individuals and provides both descriptive, and more recently, predictive tools to better understand the social dynamics of group living species (Wilson, Krause, et al. 2014). Moreover, recent conceptual and analytical advances have made it possible to circumvent troublesome obstacles for network research in the wild including 1) dealing with missing or unseen individuals in network observations, 2) enabling comparisons of networks with different properties (e.g., number of individuals, interactions), and 3) relating social patterns to underlying mechanistic dynamics (Wilson, Krause, et al. 2014). Such advances are imperative for studies of large or highly mobile and free-ranging species where direct observations and data collection might only be possible through transects, scan-sampling or infrequent surveys/captures, and where missing data points or individuals are highly probable when sampling. Additional advances in network research have made it possible to study network attributes (e.g., network position) in the context of personality (Wilson et al. 2013), adding a significant investigative layer by which to study individual-based differences in behavior and how these relate to social processes (e.g., frequency and longevity of social relations) (Krause et al. 2010; Wilson, Croft, et al. 2014).

Despite the conceptual innovations and enormous application potential of electronic sensor tags for ecological research, as yet none to our knowledge have attempted to use such tags in conjunction with direct observations of personality and network analysis in an aquatic species (but see Jacoby, Brooks, et al. 2012; Jacoby, Croft, et al. 2012). This gap in our current state of knowledge is directly attributable to the sampling difficulties mentioned above (crypsis, high mobility) or in the case of many predatory species—high levels of crepuscular or nocturnal activities. That said, many species, including some sharks (Wilson, Croft, et al. 2014), are amenable to this type of integrative framework, particularly those species which show relatively high site fidelity and long-term residency (Morrissey and Gruber 1993; Pratt and Carrier 2001; Guttridge et al. 2011; Mourier et al. 2012).

Here, using the lemon shark (*Negaprion brevirostris*), a comparatively well-studied and gregarious species (as juveniles in nursery areas) known to preferentially assort based on body size (Guttridge et al. 2011) and prefer groups of conspecifics over heterospecifics (Guttridge et al. 2009), we combined direct observation, accelerometry, and network analysis to better understand the mechanistic bases of sociality by characterizing individual-level differences in behavioral traits (e.g., activity, leadership). Our study therefore had 2 primary objectives. Firstly, to determine the relationship between sociality and individual differences in locomotor activity and diel movement patterns using observation and sensor tag data. Secondly, to determine how recent advances (Jacoby, Brooks, et al. 2012; Wilson et al. 2013; Wilson, Krause, et al. 2014) in network analysis could provide novel insights into shark social behavior. More specifically, our second objective was to establish whether: 1) lemon sharks consistently occupy certain positions in their networks, 2) dynamic models of interaction based on Markov chains can explain shark social dynamics, 3) sharks preferentially associate with other individuals or by sex, and lastly whether 4) similarity or nonsimilarity of behavioral traits can explain network associations in a widespread marine predator.

MATERIALS AND METHODS

We collected a population of 10 juvenile lemon sharks (67 ± 4.9 cm total length [TL] ± standard deviation, 5 males, 5 females) from a small tidal mangrove creek (24°48.9′N, 76°18.1′W), on the island of Eleuthera, the Bahamas. It is important to note that these individuals represented the majority of, if not entire, nursery population of lemon sharks in the sampled system and is representative of other wetland areas around the island of Eleuthera (Murchie et al. 2010). However, other islands in the Bahamas are known to have higher densities of these species (e.g., Bimini) (Guttridge et al. 2009). Lemon sharks were collected on 9 January 2014 by seine net and transported by boat in 90-L coolers to a nearby wetland facility for holding. These individuals were held for 3 days prior to experimentation in a large circular holding tank (3.7-m diameter × 1.25-m height; 13 180 L; flow rate 1800 L/h) and fed to satiation daily using cut fish (*Sardinella* sp.). This acclimation period was necessary to insure all individuals were feeding (to minimize risk of state-dependent changes in behavior associated with hunger levels) prior to tagging (see below). Juvenile sharks were chosen as they exhibit higher site fidelity and levels of sociality (avoid predation in the shallower waters surrounding mangrove coastal flats) and are thus better suited to our experimental design (see below) than adult sharks who are less social and do not enter such shallower waters (<1 m) unless for reproductive purposes (Morrissey and Gruber 1993; Pratt and Carrier 2001).

Tagging and wetland mesocosm

To enable individual identification and collection of locomotor activity data, lemon sharks were affixed with individually identifiable (color coded) tri-axial accelerometer loggers (model X8M-3, 500-mAh battery, 15 g in air, 25-Hz recording frequency; Gulf Coast Data Concepts, Waveland, MS) at the base of the first dorsal fin. Tags were attached using 36-kg strength braided Dacron line secured to plastic frontal and backing plates (Figure 1a). Following tagging, sharks were released in a ~2500 m^2 enclosed wetland mesocosm (Figure 1b) near the aquarium facilities of the Cape Eleuthera Institute for a period of 8 days. As above, sharks were provided cut fish (*Sardinella* sp.) daily to supplement natural foraging of prey in the wetland mesocosm and insure all test animals were healthy and eating. Presentation of supplemental food items occurred in the evenings and always more than 16 h prior to the next observation period. The wetland, while natural in origin, is enclosed and largely separated from the ocean except during extreme tides. The wetland is vegetated with red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), and various algae (e.g., *Halimeda* spp.). Resident fish species include bonefish (*Albula vulpes*), mangrove snapper (*Lutjanus griseus*), juvenile great barracuda (*Sphyraena barracuda*), and a variety of mojarra species (Gerreidae). The wetland is

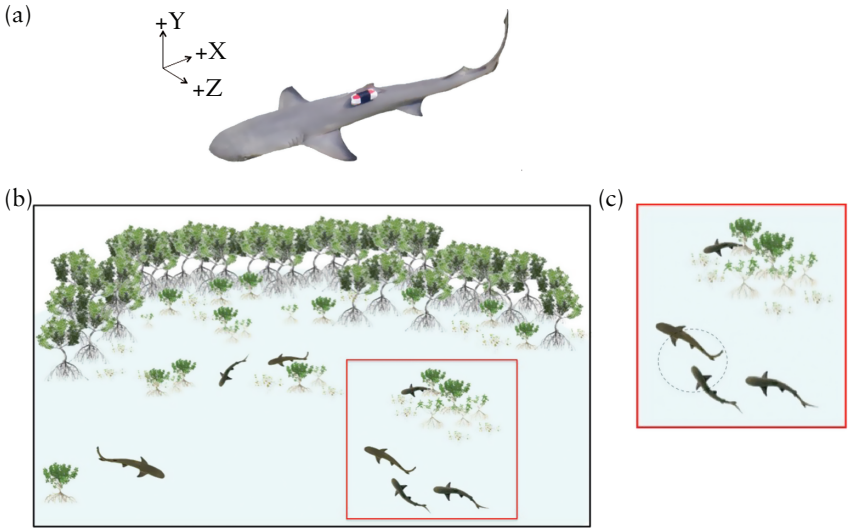

Figure 1
Photograph (a) of juvenile lemon shark with individually identifiable accelerometer tag attached to first dorsal fin. Illustrative representations of (b) wetland area where observations of shark behavior and network characteristics occurred as well as (c) an enlarged inset illustrating sharks in refuge (near mangrove roots) and actively swimming in a trio with anterior individual acting as group leader. Dotted circle in inset represents area of one body length by which individuals were said to be associating with a particular individual during observations.

also supplemented with a constant influx of fresh seawater from the adjacent wetland facility.

Behavior and network observations

Over the course of 8 days, scan-sampling observations occurred 3 times per day (early morning, mid-day, late afternoon) for several traits including individual differences in sociability/social score, leadership (tendency to be at the front of a mobile group/pair), and refuge use (Figure 1c). Sociability or the social score of an individual was assessed by the tendency for an individual to associate with (within one body length, ~1 m) 1 or more other sharks during a sampling event. Leadership was quantified as an individual being located in the front of a mobile group of 1 or more other nonfocal individuals. Lastly, refuge use was quantified as the tendency for a focal individual to be actively swimming or resting within 1 m of refuge (mangrove roots/canopy). For each observation period, all sharks were observed consecutively but independently for every sampling session (i.e., 2 continuously interacting individuals were never recorded consecutively unless more than 5 min had passed from the previous individual's focal follow). Locomotor activity data were recorded continuously by accelerometer biologgers and used to generate diel patterns in behavior as well as record individual differences in movement characteristics.

Every day during the observation period, 2 independent network sessions (see Wilson, Krause, et al. 2014 for details) were conducted between 06:45 and 08:30 in the morning, weather permitting. In total, 15 network sessions were conducted (on 1 occasion, it was only possible to collect 1 session due to high wind and surface conditions impeding visibility), and all individuals were observed for every session. This number of sessions is ideal for characterizing social network dynamics using the fission–fusion model based on Markov chains developed by Wilson, Krause, et al. (2014) (see below). Network sessions were conducted during this time period each day as environmental conditions were generally optimal for observation (wind, lighting) and sharks tended to be actively moving. For each network session, an individual shark was haphazardly chosen as a focal individual and tracked continuously for 100 s following previously established techniques. During this observation period, associations between the focal shark and the nearest group member (if present) were recorded every 10 s (Figure 1c). Sharks were characterized as associating if they were within one body length of each other at the sampling interval. In an instance where more than 1 shark was within the collection distance, the individual closest to the focal individual was chosen. Following the completion of the observation period, a separate and independent (not associating with previous focal individual in the last 100 s, if possible) was chosen as the next focal individual, until all individuals had been recorded. In this manner, all individuals were recorded for every network session.

Data analysis

Network data

In attempt to explain shark social dynamics, we used a fission–fusion model based on Markov chains developed by Wilson, Krause, et al. (2014). This model describes the social behavior common to all focal individuals as sequences of "behavioral states" and can be constructed in 2 variants that only differ by their levels of detail. In the simple variant, a focal fish can either be social (with a conspecific) or alone (no conspecific within one body length). By regarding these behavioral states as states of a first-order Markov chain, the transition probabilities between them can be estimated from the data points in our observations. In a first-order Markov chain, the next state only depends on the current state. In our case, this means, for example, that the decision of a focal fish to leave its current neighbor and to swim around independently depends solely on its current state. The simple variant of the model then predicts the distributions of the lengths of phases of social contact and of being alone. In the more detailed variant, the identities of the neighbors of the focal fish are also taken into account. In addition to the simple variant, the more detailed variant also predicts the lengths of contact phases (instances of social contact) with the

same neighbor (see Wilson, Krause, et al. 2014 for more details). It has been shown that this model (in both variants) can be used to describe the social dynamics of female guppies in the wild (Wilson, Krause, et al. 2014). That said, for our analysis, we only used the more detailed variant.

We also determined whether sharks had preferences for certain conspecifics or preferences regarding sex in the network constructed from the combined data of all 8 observation days. We used 2 different ways to quantify the tie strength of a pair of individuals i_1 and i_2 in this network, 1) according to the number of contact phases between i_1 and i_2 and 2) according to the mean duration of contact between i_1 and i_2. For the analysis, we used a randomization test where for each focal individual we kept constant the number of observed contact phases as well as their lengths and randomly assigned the identities of its neighbors. For the investigation of individual preferences, we used as a test statistic, the sum of squares of the tie strengths of all pairs of individuals, which we computed in the 2 above-described ways, and for preferences regarding sex, we used the number of contact phases between sharks of the same sex. In the absence of preferences, both test statistics should yield moderate values. Large values (among the 5% largest yielded by the randomization procedure) indicate that the observed tie strengths cannot be explained by randomly chosen neighbors.

Individual preferences were only detected in terms of the frequency of contact but not its duration (see Results), which is in accordance with the Markov chain model that predicts phase length distributions common to all individuals. Therefore, in the following analyses, we only used the number of contact phases as a measure of tie strength.

Given that there are individual preferences, we additionally tested whether similarity regarding behavioral traits is an explaining factor in associations following the methodology described in Wilson, Krause, et al. (2014). Trait "similarity" was defined using a tolerance level t. For example, for a tolerance level of $t = 0.1$ and the attribute "mean swimming duration," all fish were regarded as being similar to the focal individual if they had a mean swimming duration that did not deviate by more than 10% from that of the focal shark. For each focal fish, we computed the percentage of contact phases it had with other fish that were similar to it regarding a given trait. The sum of these percentages determined the value of the test statistic. In contrast to the Wilson, Krause, et al. (2014) methodology, we tested for behavioral traits being an explaining factor in associations based both on similarity and nonsimilarity, meaning that our tests were 2 sided and P values were regarded as significant if $P < 0.025$ (for similarity) or $P > 0.975$ (for nonsimilarity). For example, should the sum of percentages of contact phases be significantly greater than expected, we can conclude that there is assortment by similarity (regarding the trait under investigation). Similarly, a sum of percentages of contact phases that is smaller than expected suggests that similar individuals tend to avoid each other and prefer individuals that differ regarding the trait (e.g., followers demonstrating a preference for leaders). Following Wilson, Krause, et al. (2014), we regarded an attribute as an explaining factor if the test statistic had significant values for a range of tolerance levels that corresponded to a range of percentages of individuals regarded as similar of size 10 or more.

To assess if individual sharks consistently occupy positions within their social networks, we followed a conceptual framework recently described by Wilson et al. (2013), which is based on randomization techniques and uses as a test statistic the variances of the ranks of individual network positions across the networks. As per the previously established protocol, we tested for consistency in network positions across the 8-day networks (sessions combined each day separately) using node strength, weighted node betweenness, and weighted clustering coefficient as network metrics. Weights were calculated based on the number of contact phases between individuals.

Accelerometry and behavioral data

To examine the mechanistic bases of sociality and to examine both intrinsic and extrinsic predictors of accelerometer-measured lemon shark behavior, we used multilevel models to predict 1) proportion of time spent swimming, 2) proportion of time spent swimming fast, and 3) number of swimming periods (bursts and transitions between activity states) with explanatory variables including: *diel period*, *social score* (sociability), *refuge use*, *size* (TL), *sex*, *individual ID*, and *study hour*. Leadership was not included in the model due to strong collinearity ($r = 0.8$) with social score. For proportion of time spent swimming and proportion of time spent swimming fast, we used binomial generalized linear mixed-effects models (GLMM) where the intercept for fish ID was allowed to vary for each individual. Because the final models were overdispersed, we also included an observation-level random effect (Breslow 1990; Maindonald and Braun 2010). To choose the optimal model, we used single-term deletions and backwards selection (drop1 command, Chambers 1992) to find the least significant term at $P < 0.05$ (Zuur et al. 2009). To evaluate normality, heteroscedasticity, and independence, we examined for patterns in the normalized residuals and plotted the residuals against all variables, including those not in the final model. Models were implemented using the package lme4 in the R statistical environment (Pinheiro and Bates 2000; Team RDC 2012). Number of transitions was first modeled using a GLMM where fish ID was a random factor and the response was assumed to follow a Poisson distribution. Due to strong nonlinear patterns in the normalized residuals using GLMM, we opted to model number of transitions using a generalized additive mixed-model (GAMM; Wood 2006; Zuur et al. 2014) with a cyclic penalized cubic regression spline smooth for hour of the day ($n = 24$). A manual drop1 procedure was performed for GAMMs (Zuur et al. 2009). The final model was validated using the procedure outlined for the GLMMs. Autocorrelation plots indicated residuals were highly correlated along the time series (hour), thus a moving average correlations structure was added to reduce serial autocorrelation (Pinheiro and Bates 2000; Zuur et al. 2009).

Sensor tag data

Tri-axial accelerometers continuously recorded total acceleration (g, 9.8 m/s^2) at 25 Hz in 3 axes (x = surge, y = heave, z = sway), where total acceleration is the sum of static (gravity) and dynamic (shark movement) acceleration with maximum values of ±8 g. Static and dynamic acceleration were separated using a weighted smoothing interval of 2 s. The appropriate interval was determined as per Shepard et al. (2009). Individual lemon shark behaviors were identified from acceleration data using continuous wavelet transformation on the z axis (sway) dynamic acceleration including a band-pass filter for frequencies of 0.3–10 Hz. A k-means clustering algorithm was then used to identify similar spectra as nonswimming (resting or drifting; low amplitude [<0.026 g], noncyclic waveforms; Brownscombe et al. 2014) or swimming (≥0.026 g amplitude, cyclic waveforms) behaviors. The algorithm also identified distinct, higher-intensity swimming behaviors that were further defined as fast (≥0.06 g amplitude) and burst (≥0.1 g amplitude) swimming. Transitions between swimming and nonswimming behaviors

(Figure 2) were also quantified as a measure of intermittent locomotion (Kramer and McLaughlin 2001; Wilson and Godin 2010). Acceleration data analysis was conducted using Igor Pro 6.32 software (WaveMetrics Inc., Lake Oswego, OR) and Ethographer (Sakamoto et al. 2009).

RESULTS

Network analysis and behavior

Our analyses revealed that Markov chain models can explain shark social dynamics quite well, particularly with respect to length of contact with particular neighbors (Figure 4a), social contact in general (Figure 4b), and time spent swimming alone (Figure 4c). Sharks demonstrated distinct preferences for certain conspecifics when tie strength was defined by the number of contact phases ($P = 0.017$, number of randomization steps = 10^4, test statistic sum of squares of tie strengths, Figure 3) but not mean length of contact ($P = 0.26$, number of randomization steps = 10^4, test statistic sum of squares of tie strengths). Further analyses revealed that this result can be explained, in part, by sharks preferentially associating with conspecifics of the same sex ($P = 0.025$, number of randomization steps = 10^4, test statistic number of contact phases between sharks of the same sex).

Additional detailed analyses of the social fine structure of this population suggested that sharks positively assort based on similarity for proportion of time spent swimming fast and mean swimming duration as explaining factors. Similarly, our analyses also suggested that sharks associated based on nonsimilarity regarding leadership as well as frequency of burst swimming events and number of transitions between activity states (Table 1). Irrespective of network metric, sharks did not demonstrate consistency in network position across observation days (Supplementary Table 1, $P = 0.65$ for node strength, $P = 0.57$ for node betweenness, and $P = 0.31$ for the clustering coefficient, number of randomization steps = 10^5).

Accelerometry and behavior

Lemon sharks exhibited diverse behavioral patterns between individuals and across environmental factors while in the wetland. Diel period, social score, TL, sex, refuge use, and the interaction between social score and sex were all significant predictors of lemon shark swimming activity (Tables 2 and 3). Holding refuge use and centered TL at their means, the GLMM illustrated that although the least social sharks (male and female) were equally likely to be active at night (♂: 0.451 ± 0.03 standard error [SE]; ♀: 0.457 ± 0.04 SE), more social sharks exhibited different patterns of swimming behaviors during nighttime hours (Supplementary Figure 1). At night and compared with relatively unsocial individuals, swimming activity was predicted to be greatest in highly social males (0.505 ± 0.06 SE) whereas lowest for highly social females (0.372 ± 0.06 SE). Similar to the night, low social scoring males and females were predicted to exhibit similar probabilities for general activity (♂: 0.364 ± 0.04 SE; ♀: 0.370 ± 0.04 SE). Again, more social males were more likely to exhibit increased activity during the daylight hours (0.416 ± 0.07 SE) whereas more social females were less likely to be active (0.293 ± 0.06 SE; Figure 1).

The final model for proportion of time spent swimming fast contained only diel period as a marginally significant explanatory variable ($P = 0.026$, Table 2). Here, lemon sharks are predicted to be slightly (3.1%) more likely to exhibit fast swimming behavior during the night compared with during the day (Table 2). The final model for number of transitions contained 7 terms including the highly significant dependency structure (Tables 2 and 3). In addition, the smoothing term was highly significant ($F = 4.32$, $P < 0.0001$, Supplementary Figure 2). The smoothing function indicated that time of day was strongly related to this behavior such that the number of transitions increased from approximately 11:00 AM to midnight then decreased sharply until approximately 5:00 AM (Supplementary Figure 2).

DISCUSSION

Group living is a well-studied phenomenon having been documented extensively in numerous terrestrial, freshwater, and marine species (Krause and Ruxton 2002). However, while in some taxa, teleost fishes for example, a great deal is known with respect to underlying proximate and ultimate bases of these social processes, comparatively little is known about the underpinnings of this behavior in elasmobranchs (Jacoby, Croft, et al. 2012; Wilson, Croft, et al. 2014). In fact, until relatively recently the best sources of information on social behavior in sharks were largely speculative and observational in nature (but see Jacoby et al. 2010; Guttridge et al. 2011; Mourier et al. 2012; Jacoby et al. 2014). Using a novel combination of recent advances in network analysis, sensor tag data and direct observation, we provide some of the first information on the mechanistic bases of group living and personality (sociability,

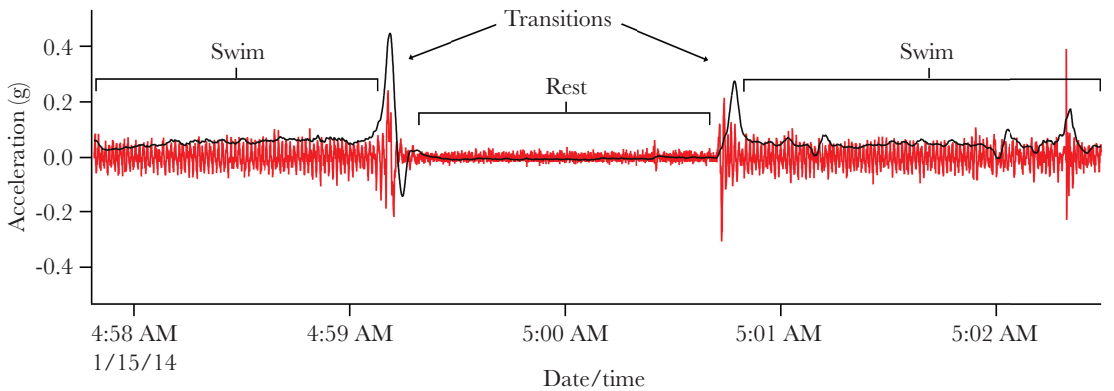

Figure 2
Visualization of lemon shark transitions between swimming and resting behaviors in dynamic sway (tail beats; red) and surge static (body pitch; black) acceleration measured using tri-axial accelerometer loggers.

activity patterns, refuge use) in a gregarious life-history stage of wild sharks. Importantly, our integrative approach and analyses provide new insights into shark ecology by highlighting links and patterns in social behavior as well as its mechanistic underpinnings based on activity data.

Although teleost fishes are known to assort based on size, coloration, parasite load, familiarity, and kinship (Krause et al. 2000), empirical studies on the mechanistic bases of assortment in elasmobranchs are scarce (but see Guttridge et al. 2011; Mourier et al. 2012 for examples). For example, juvenile lemon sharks are known to preferentially assort based on body size (Guttridge et al. 2011) and prefer groups of conspecifics over heterospecifics (Guttridge et al. 2009). Our results also found evidence of active partner preference in lemon sharks through repeated associations based on individual preference (in terms of frequency but not duration of contact) for same-sex group members (Figure 3). Although we did not observe evidence in support of assortment by size, this might be attributable, in part, to our low overall range of body sizes between sharks. Alternatively, another possible mechanistic explanation for individual preference for certain conspecifics might be that sharks assort based on energetic profiles or activity budgets (Wearmouth and Sims 2008). Indeed, our sharks were observed to preferentially associate with individuals based on similarity (proportion of time spent swimming fast and mean swimming duration) or nonsimilarity (number of burst swimming events and number of transitions between activity states) for a number of locomotor traits, some of which were associated with other behavioral attributes (e.g., leadership, nonsimilarity; Figure 3). Similarly, our sensor tag analyses revealed that social sharks exhibited different diel swimming patterns from less social sharks and further that this relationship varied between sexes, with social males being more active than social females. We also noted distinct differences between sharks in terms of numbers of transitions between activity states and overall locomotor profile. This notion of locomotor or energetic profiles being associated with social attributes might also be indicative of behavioral type assortment as it has previously been shown that fish exhibit patterns of consistent variation in bouts of activity versus pauses and further, that this variation correlates with their personality (intermittent locomotion, Wilson and Godin 2010). As such this might tie into consistent differences in transitions between activity states (fast versus slow swimming) and types (e.g., bursts versus casual swimming) as observed here.

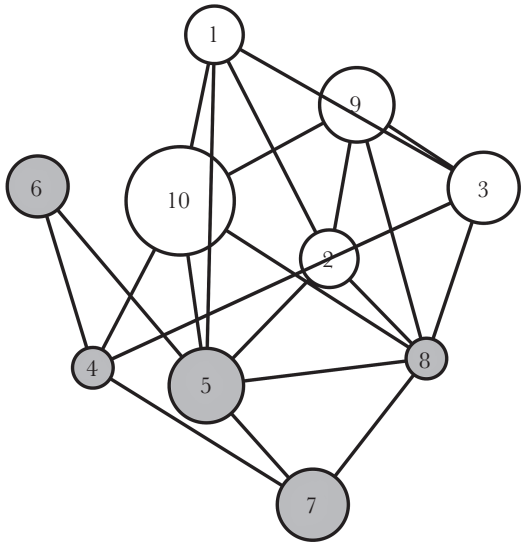

Figure 3
Network constructed from the combined data of all 8 observation days, where the tie strength was defined by the number of contact phases. The areas of the nodes are proportional to the leadership score of the individuals they represent. The gray nodes represent the males. To make the structure clearer, edges with weights smaller than the median weight are not shown. However, the spring layout was computed taking all edges into account.

In addition to preference for certain individuals, we also found that lemon sharks preferentially associate by sex. Sex segregation is comparatively well studied across sharks (Klimley 1987; Sims et al. 2001) and is thought to be common due to intersexual conflict and conflicting life-history needs between sexes through ontogeny (Jacoby et al. 2010). Additionally, the onset of such segregation can occur at a relatively early ages in some species, preceding sexual maturation (Litvinov 2006), as found here. Lastly, individual preferences might also be associated with differences in familiarity (previous experience) or kinship (genetic relatedness). These sharks were collected from the same geographical location at the same time, and sharks in this region exhibit high site fidelity, often returning

Table 1
Assortative behavior within the social network constructed from the combined data of all 8 observation days for a number of behavioral traits

Behavior	Assortment by similarity		Assortment by nonsimilarity	
	Tolerance level	% individual pairs within tolerance	Tolerance level	% individual pairs within tolerance
Social score	—	—	—	—
Refuge use	—	—	—	—
Leadership	—	—	0.42–0.52	38–49%
Body length	—	—	—	—
Proportion of time spent swimming slow	—	—	—	—
Proportion of time spent swimming fast	0.56–3.93	46–92%	—	—
Frequency of burst swimming events	—	—	0.32–0.52	29–52%
Number of transitions between activity states	—	—	0.27–5.77	17–90%
Mean swim duration	0.95—4.20	54–78%	—	—
Proportion of time spent swimming (general activity)	—	—	—	—

Indicated are the range of tolerance levels (i.e., by how much individuals were different regarding a given behavioral trait) where the test yielded P values < 0.025 (similarity) or $P > 0.975$ (nonsimilarity). The corresponding percentages of pairs of individuals that were regarded as similar given the tolerance level are also shown.

Table 2

Results from the backwards model selection procedure for each of the models including the GLMMs for proportion of spent time swimming (%Swimming) and proportion of time spent swimming fast (%Fast), and for the GAMM for number of transitions between activity states (Num. of Trans.)

Response	Term removed	df	AIC	LRT	*P* value
%Swimming	None—full model		2658		
	Diel	1	2828	172.425	<0.0001
	TL	1	2662	5.9	0.015
	Refuge	1	2670	13.9	<0.001
	Social score × sex	1	2668	12.0	<0.001
%Fast	None—full model		4552.2		
	Diel	1	4555.2	4.97	0.026
Num. of Trans.	None—full model		2509.9		
	Centered TL	1	2541.6	16.84	<0.0001
	Refuge use	1	2542.9	17.49	<0.0001
	Sex:social score	1	2552.8	22.47	<0.0001
	Diel:social score	1	2535.8	13.96	<0.0001
	Cor	7	2883.4	193.8	<0.0001

P values are calculated from the chi-square distribution. AIC scores also illustrate that the best model contains all terms. The model for number of transitions shows the significance of the autoregressive correlation structure (*Cor*). AIC, Akaike information criterion; df, degrees of freedom; LRT, log-ratio test.

Table 3

Summary statistics for fixed effects for the best models that explain proportion of time spent swimming (%Swimming), proportion of time spent swimming fast (%Fast), and the number of transitions between activity states (Num. of Trans.)

Response	Fixed effect	Estimate	SE	Statistic	*P* value
				z value	
%Swimming	Intercept	−0.448	0.033	−13.57	<0.0001
	Diel—night	0.359	0.026	13.70	<0.0001
	Centered social score	−0.829	0.321	2.582	0.01
	Centered TL	−0.013	0.005	−2.45	0.014
	Sex—male	−0.258	0.048	−5.37	<0.0001
	Centered refuge use	−3.08	0.696	−4.44	<0.0001
	Centered social score × sex—male	−2.18	0.562	−3.88	<0.001
%Fast	Intercept	0.706	0.218	3.232	0.001
	Diel—night	−0.138	0.062	−2.230	0.025
				t value	
Num. of Trans.	Intercept	2.62	0.490	5.34	<0.0001
	Diel—night	−0.067	0.131	−0.51	0.612
	Social score	−13.07	5.206	−2.51	0.012
	Centered TL	0.255	0.085	3.00	0.003
	Sex—male	1.661	0.755	2.20	0.028
	Centered refuge use	28.28	10.97	2.58	0.010
	Diel—night × social score	0.747	0.955	0.782	0.434
	Sex—male × social score	23.66	8.539	2.77	0.006

the same locations as they were born to reproduce (Morrissey and Gruber 1993). Therefore, it is possible that the sharks comprised members of a litter cluster (2 or more litters) in this nursery area and were likely all familiar to some extent prior to our study (Chapman et al. 2009) although additional trials with individuals from different populations would be necessary to ascertain this experimentally and we did not conduct any genetic sampling to test kinship. That said, genetic relatedness might be an unlikely sole explanation of our findings as we did not find associations based on size (a main indicator of age class) but instead primarily by sex.

To test for individual consistency in network positions, we applied the test outlined in Wilson et al. (2013). This test requires that the observation probabilities of all individuals in a given network be equal, which was the case in our study. Additionally, we analyzed individual preferences using a randomization test where we kept constant the number of observed contact phases and their lengths randomly assigned to the individuals' identities. However, despite our initial objective, we did not observe any consistency in network positions in the any of the network metrics used. That said, when present, consistency in network position likely has important consequences for understanding aspects of social behavior or personality due to the costs associated with achieving and maintaining certain positions within a network (e.g., group leader) as well as individual fitness (via transmission of information, disease, and genetic information) (Wilson et al. 2013). It is possible that our transplantation of this population of sharks to the wetland mesocosm disrupted aspects of consistency in the shark network; however, a recent study on the small-spotted

catshark, *Scyliorhinus canicula*, found that network positions can be surprisingly consistent and repeatable even in changing environments (Jacoby et al. 2014). Similarly, some preliminary work on teleosts also seems to suggest that network position consistency can be robust to manipulation, including population transplantation (Wilson et al. (2015)). However, given the current scarcity of published data on this topic, more data will be needed to interpret our results in a broader context.

We also used a fission–fusion model based on Markov chains to better understand the underlying dynamics of the social behavior of juvenile lemon sharks. This approach worked quite well, with our model explaining general length of contact with particular neighbors as well as tendency for being social/asocial (Figure 4). In fact, in many respects lemon shark social dynamics very closely mirror those of wild guppies (*Poecilia reticulata*) inhabiting small freshwater pools, for which the Markov approach was initially developed (Wilson, Krause, et al. 2014, Table 4). Ongoing research on both taxa suggests that the social dynamics of these 2 systems both follow geometric (or negative exponential) distributions that might be a result of strong selection pressure favoring behavioral responses, which are difficult for predators to track/predict (Wilson, Krause, et al. 2014). Such compelling results perhaps suggest the broad applicability and usefulness for this approach in understanding the dynamic interactions occurring in animal social systems in general and therefore, warrants further study.

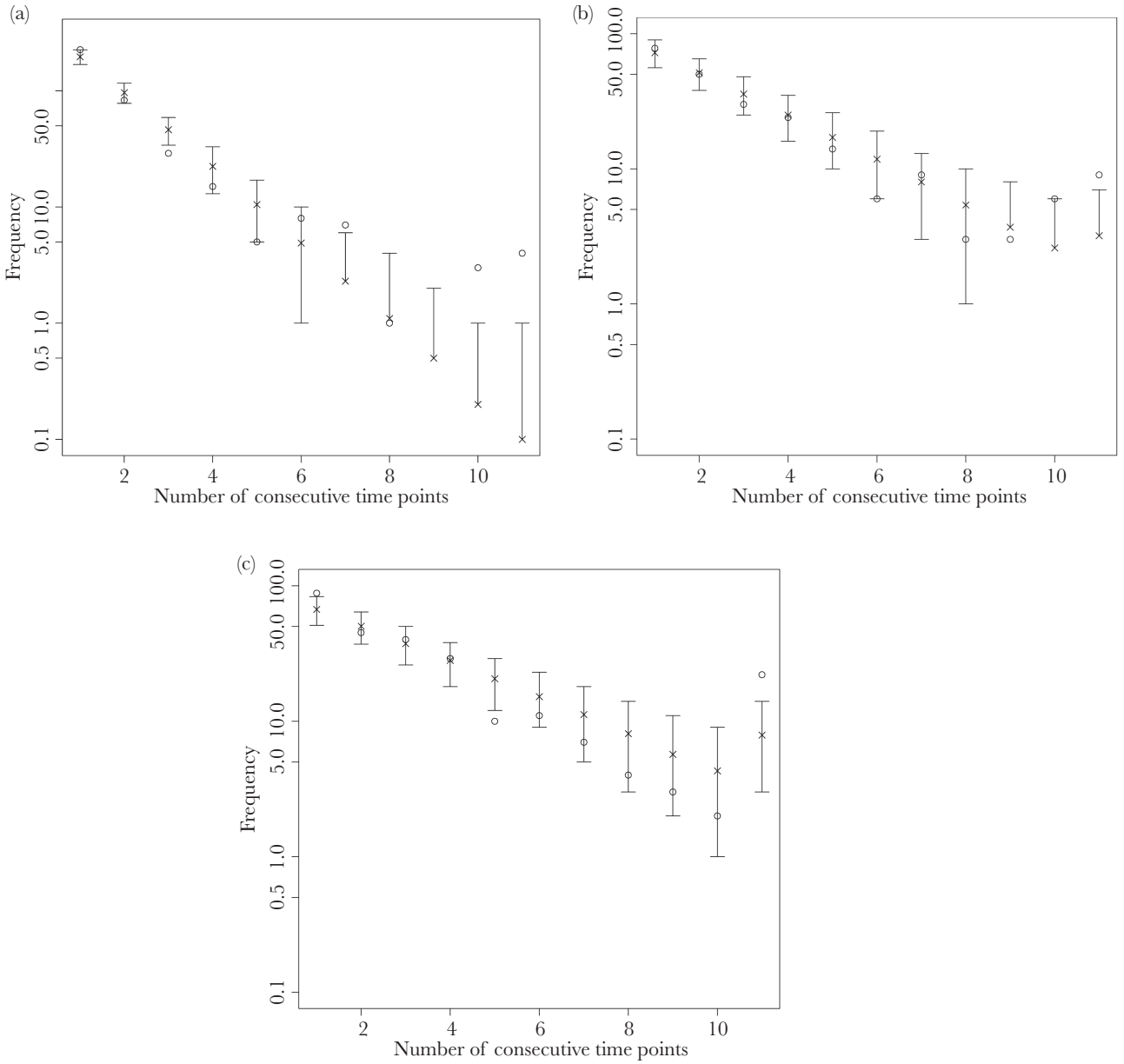

Figure 4

Frequency distributions of (a) lengths of contact with a particular nearest neighbor, (b) lengths of social contact in general (i.e., the number of successive times a focal individual was in close proximity to a neighbor), and (c) the lengths of time an individual spent swimming alone in the observed data (circles). Also shown are the means (shown as "×") and the 2.5% and 97.5% percentiles as predicted by our Markov chain model.

Table 4

Comparative data on frequency of social dynamics from lemon sharks in the current study as well as 2 wild populations of Trinidadian guppies, *Poecilia reticulata*

	Lemon sharks	Guppies (Wilson, Krause, et al. (2014) all female)	Guppies (Wilson et al. 2015 "pool 3"; males and females)
Proportion of time spent being social	45%	40%	20%
Mean length of social contact	39 s	31 s	17 s
Mean length of swimming around alone	48 s	50 s	69 s
Number of different nearest neighbors per social contact phase	1.9	1.6	1.2

Although our study focused on a single representative population of juvenile lemon sharks, our findings and experimental technique in particular can be used as a platform to build on for further research on the social behavior of gregarious elasmobranchs. Our study is the first to use an integrative approach based on concurrent application of network analysis, accelerometry, and direct observation to better understand shark ecology and behavior. We provide novel evidence with regard to shark sociability and its mechanistic bases through preferential assortment by sex, individual preference, and similarity/nonsimilarity for various behavioral and locomotory traits. Our use of accelerometer tags to continuously monitor shark movements also ties these results together in the context of diel patterns of behavior and how this might differ between sexes, even when direct observation of test individuals is not always possible (Brown et al. 2013). Although acoustic telemetry is more common in shark studies (Guttridge et al. 2010; Jacoby, Croft, et al. 2012), accelerometer biologger tags offer a unique opportunity to characterize individual differences in activity at continuous, extremely fine scales (Brown et al. 2013) as well as combine estimates of energetic budgets and locomotor patterns to provide new insights into shark behavior. When combined with direct observations of behavior and network approaches, such technology can therefore be an effective tool for better understanding free-ranging shark ecology, particularly with juvenile elasmobranchs that commonly aggregate in near shore, shallow habitats (Knip et al. 2010). We suggest that such integrative fine-scale approaches represent powerful tools capable of providing new insights and understanding regarding the social dynamics of elasmobranchs and other taxa.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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